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Vision Research 47 (2007) 3141–3149
Vision Research
www.elsevier.com/locate/visres

Adaptation duration affects the spatial selectivity of facial aftereffects

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Received 14 December 2006; received in revised form 8 August 2007

Abstract

Adaptation processes in human early visual cortical areas are sensitive to the exposure time of the adaptor stimulus. Here we investigated the effect of adaptation duration at the higher, shape-specific stages of visual processing using facial adaptation. It was found that long-term (5 s) adaptation evokes facial aftereffects consisting of a position invariant as well as a position-specific component. As a result of adaptation to a female face, test faces were judged more masculine when they were displayed in the same location as the female adaptor face, as compared to that when they were presented in the opposite visual hemifield. However, aftereffects evoked by short-term (500 ms) adaptation were found to be entirely position invariant. In accordance with these behavioral results, we found that the adaptation effects, measured on the amplitude of the N170 ERP component consisted of a position-specific component only after long-term, but not after short-term adaptation conditions. These results suggest that both short and long exposure to a face stimulus leads to adaptation of position invariant face-selective processes, whereas adaptation of position-specific neural mechanisms of face processing requires long-term adaptation. Our findings imply that manipulating adaptation duration provides an opportunity to specifically adapt different neural processes of shape-specific coding and to investigate their stimulus selectivity.

Keywords: Face processing; Event-related potentials (ERPs); Timing; Human; Position invariance; Translational invariance

1. Introduction

Adaptation is a common property of neurons at all levels of the visual processing. Repetition of a particular stimulus usually lowers the firing rate of the responsive neurons and reduces the blood oxygen-level dependent (BOLD) responses (for reviews see Grill-Spector, Henson, & Martin, 2006; Krekelberg, Boynton, & van Wezel, 2006), in experiments of extracellular single-cell recordings and functional magnetic resonance imaging (fMRI)[1] measurements, respectively. One of the important parameters affecting the site of adaptation is its timescale, i.e. the exposure time of the first (adaptor) stimulus (Krekelberg et al., 2006).

In psychophysical experiments of mid-level adaptation it has been shown that shape contrast—which is a negative aftereffect for simple shape properties (i.e. convex or concave contours)—can also be induced by short (<1 s) adaptation (Suzuki & Cavanagh, 1998). All other previous studies reporting shape-specific aftereffects used a prolonged adaptation period, lasting for several second or even for minutes. In fact, Leopold et al. (Leopold, O'Toole, Vetter, & Blanz, 2001) reported that short adaptation failed to evoke identity specific facial adaptation.

Using fMRI it was found that adaptation to basic visual features (such as orientation) at the early, retinotopically organized visual cortical areas—in particular in the primary visual cortex—can be revealed only after long-term

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[1] *Abbreviations used:* ERP, event-related potentials; fMRI, functional magnetic resonance imaging.

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doi:10.1016/j.visres.2007.08.019

exposure (several seconds) to the adapting stimulus (Fang, Murray, Kersten, & He, 2005). This is in sharp contrast to what was found in the later, more downstream visual cortical areas (i.e. V4, LO, IT) where not only long-term, but already very short adaptation (less than 1 s, the so called fMRI adaptation procedure) to specific features or objects can evoke strong fMRI adaptation effects (Henson, 2003a). These results suggest that different neural populations along the visual hierarchy might differ in their dynamics of adaptation. If this is so, it raises the intriguing possibility that by manipulating adaptation duration one can selectively adapt neural processes at different stages of visual processing and investigate their stimulus selectivity.

In the present study we investigated short- and long-term adaptation effects at the higher, shape-specific stages of visual processing using face adaptation (Leopold et al., 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999; Yamashita, Hardy, De Valois, & Webster, 2005). Recently, Leopold, Rhodes, Müller, and Jeffrey (2005) has shown that varying the duration of the adapter affects face adaptation; the strength of face identity aftereffect increases as a function of adaptation time. Earlier fMRI (Andrews & Ewbank, 2004; Henson, 2003a), ERP (Henson et al., 2003b; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Trenner, Schweinberger, Jentzscha, & Sommer, 2004) and MEG (Boehm, Sommer, & Lueschow, 2005; Harris & Nakayama, 2006) studies used short-term adaptation to investigate face specific processing and found strong adaptation effects. However, the neuroimaging results concerning the effect of adaptation duration on the strength of adaptation are less conclusive and suggest that it might depend on the type of the stimuli used as well as on the testing protocol. For example, Sayres and Grill-Spector (2006) found, that the magnitude of repetition related BOLD response suppression increases gradually with the number of repetitions, whereas Zago, Fenske, Aminoff, and Bar (2005) found, that BOLD response reduction is maximal for relatively short (40–250 ms) exposition times, while longer (up to 1900 ms) presentations lead to the reduction of the effect. Importantly, Fang, Murray, and He (2006) have shown that adaptation duration can also affect the properties of fMRI adaptation effects: while long-term (5000 ms) adaptation effects were found to be selective to the viewpoint of the face, short-term (300 ms) adaptation effects were viewpoint independent along the ventral pathway, including the lateral occipital cortex and right fusiform area.

Here we used event related potentials (ERP) to investigate the effect of adaptation duration on the strength and properties of facial adaptation effects, as well as on their electrophysiological correlates. In a recent study, we have shown that long-term face adaptation has a strong effect on the ERP responses and that it is the N170 component that represents the primary ERP correlate of long-term face adaptation (Kovács et al., 2006). Moreover, we also have shown that both the behavioral face adaptation effects as well as their ERP correlates consist of position-specific and position-invariant components (Kovács, Zimmer, Harza, Antal, & Vidnyánszky, 2005), reflecting adaptation processes of neural populations with different positional sensitivity. The goal of the present study was to test whether adaptation duration differentially modulates the position-specific and position-invariant components of the behavioral face aftereffects as well as the ERP correlates of face adaptation. Based on the fMRI results suggesting that adaptation of neural processes at the earlier stages of visual cortical processing need longer adaptation period than that at the higher stages of visual processing we predicted that: position-specific ERP face adaptation effects can be evoked only by long-term (5 s) adaptation, whereas the position-invariant component will be present both after short- (500 ms) and long-term adaptation.

2. Materials and methods

The stimuli, the task, the long-term adaptation condition and the electrophysiological recording procedures were identical to those used and described in details in recent studies by Kovács, Zimmer, Harza, Antal, and Vidnyánszky (2005) and Kovács et al. (2006) thus here just a brief description of these and additional details are given.

2.1. Experimental subjects

Twenty-one naïve, healthy volunteers (9 females) with normal or corrected-to normal vision participated in the experiments (mean age: 22 ± 2 years). The procedures were approved by the Ethical Committee of the Budapest University of Technology and Economics.

2.2. Stimuli and procedures

The stimuli were derived from three female and male face pairs, morphed into each other. Gray-scale images, corresponding to 0% female/100% male, 12%/88%, 24%/76%, 36%/64%, 48%/52% and 52%/48%, 64%/36%, 76%/24% 88%/12%, 100% female/0% male faces were used. The Fourier phase randomized versions of the stimuli were created by an algorithm (Nasanen, 1999) that replaces the phase spectrum with random values (ranging from 0 to 360 deg), leaving the amplitude spectrum of the image intact, while removing any shape information. The faces were fit behind an oval mask (fit into a square of 400×400 pixels, 7.3 deg) eliminating the outer contours of the faces.

A simultaneously presented face and a Fourier image, displayed peripherally 5 deg to the left and to the right from the fixation point was used as test stimulus (Fig. 1).

In the Control adapting condition, two Fourier images were presented bilaterally as adaptors, while in the long-term adaptation conditions one of the adaptor images was always the same 100% female face. Adaptors were displayed for 5 s. During the test phase, one Fourier image and a test face was displayed on the left and right of the fixation spot (closest edge 8 deg on the side) symmetrically. In one condition the side of the adaptor and test faces was the same (SAME), overlapping each other, whereas in the other condition they were presented in the opposite hemifields (DIFFERENT).

For the short-term adaptation condition we manipulated the shape information content of the image by randomising the Fourier phase of the images in the following ranges: 315, 270, 225, 180, 135, 90 and 45 deg (Nasanen, 1999). This results in eight images, where the 0 deg randomized image is the original face, and the images with increasing randomization-range contain gradually less and less of the original shape information. In the short-term adaptation condition 360 deg Fourier phase randomized adaptors were presented for 4500 ms, after which one

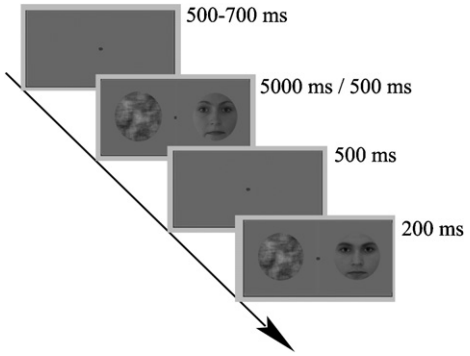

Fig. 1. Procedures and example stimuli. Timeline depicts the adaptor stimulus and an example (SAME) test stimulus.

of the images (chosen randomly either on the left or on the right side) was replaced consecutively by a 315, a 270, a 225, a 180, a 135, a 90, a 45 deg randomized image and finally by a face image which phase was not randomized (each image appeared for 100 ms). This led to a percept of a face gradually emerging from a noise field. Pilot studies showed, that gender discrimination is at chance level for images above 180 deg phase randomization, meaning a total time of gender-specific facial adaptation of approximately 500 ms.

In all three conditions (Control, short- and long-term adaptation), adaptors were followed by a 500 ms gap, and then by the test stimulus, presented for 200 ms (Fig. 1). Subjects fixated a dot in the centre while their eye-movements were controlled by an infrared eye-tracking system (IView X RED, SMI, Germany). In the further analysis we only included those trials where the fixation stayed within a 2 deg radius circle of the fixation spot (the mean ratio of valid trials across our subjects was: $87.4 \pm 5\%$, $89.1 \pm 5.4\%$ and $87.9 \pm 5.3\%$ for the Control, short- and long-term adaptation conditions (mean $\pm$ SE)). The various morph-levels were presented according to a method of constant stimuli. Subjects' task was identical in all conditions: they had to perform a two-alternative forced choice gender discrimination task. We measured the ratio of female and male responses as dependent variable. Control, short-term and long-term adaptation trials were given in separate blocks (the order randomized across subjects). Within a block (consisting 120 trials), the different types of adaptors (SAME and DIFFERENT) and the hemifield of the test stimuli (left, right) were presented randomly.

ERPs were recorded via 25 Ag/AgCl electrodes placed according to the 10/20 system (ground: left earlobe, reference: F5; impedance <5 kΩ). The EEG was offline segmented (Vision Analyser, Brain Products GmbH, Munich, Germany), into 1100 ms long trials, using a 100 ms prestimulus interval, blinks, movements, A/D saturation or EEG baseline drift were removed and the ERPs were averaged separately for each subject, condition and channel. Averages were digitally filtered (0.1–70 Hz) and average re-referencing was calculated.

2.3. Data analysis

Psychophysical data were modelled by a Weibull psychometric function, using the *psignifit* toolbox (ver. 2.5.6) for Matlab (http://bootstrap-software.org/psignifit/). First, to test whether adaptation to faces or to Fourier phase randomized images of faces results in differential effects on subsequent facial gender discrimination a three-way analysis of variance (ANOVA) was performed on the subjects' female–male decisions with the adaptation condition (Control, SAME vs. DIFFERENT; 3), male–female pairs (3) and morph level (10) as within subject factors, separately for the short- and long-term adaptation blocks. Next, to test directly the effect of adaptation duration a four-way ANOVA was performed with adaptation duration (short, long; 2), position of the adaptor and test stimuli (SAME, DIFFERENT, 2), male–female pairs (3) and morph levels (10) as factors.

To determine the onset of adaptation effects we made a point by point paired t-test on the ERP curves for each hemisphere ($p < 0.05$ for at least 30 consecutive points), across subjects and electrodes.

The amplitude and latency of the N170 was measured at six occipito-temporal electrode positions (P7/P8, PO7/PO8 and PO9/PO10) (Rossion et al., 2000), while P100 was measured on O1 and O2 electrodes. In order to determine adaptation effects, we used adaptation condition (3; Control, SAME, DIFFERENT) as factors in a one-way ANOVA separately for each hemispheres and for short- and long-term adaptation conditions. Post-hoc t-statistics were performed by Fisher LSD tests.

Finally we correlated the behaviorally and electrophysiologically observed adaptation effects. First, we determined the gender category border at 50% chance performance for each subject and each adaptation condition separately. Second we calculated the magnitude of adaptation by subtracting the stimulus morph level at the perceived category border in each adapted condition (SAME, DIFFERENT after long and short adaptations) from that of the Control condition. The electrophysiological adaptation effect was calculated by subtracting the N170 and P100 amplitude obtained during the adapted conditions from that of the Control condition. These adaptation effects were then correlated to each other by Pearsons tests.

3. Results

3.1. Behavioral results

After being adapted to a female face for 5 s the test faces were perceived more masculine as compared to the Control (Fig. 2; main effect of adaptation condition: $F(2, 1650) = 135$, $p < 0.00001$). However, the magnitude of the adaptation, reflected in the shift of the psychophysical curves along the X axis, was significantly larger when the adaptor and the test faces were presented on the same side of the fixation as compared to when they were presented in the opposite hemifields ($p = 0.00003$, post-hoc t-test). This is in accordance with our previous results

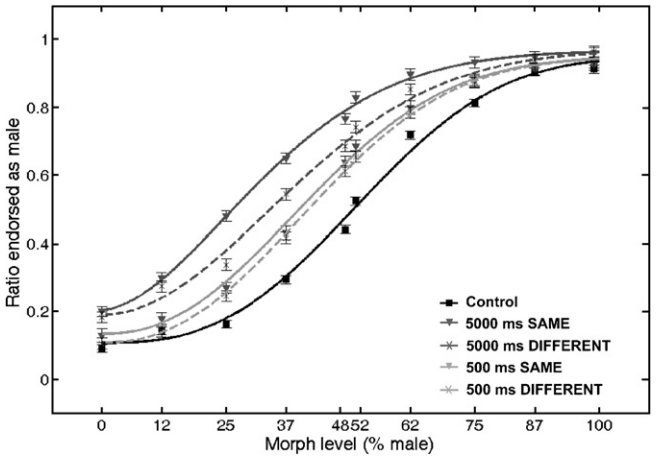

Fig. 2. Female face adaptation. Mean ratio of male responses as a function of gender morph level (% male) in Experiment I. Results with control (thick line) long-term (dark lines) and short-term (gray lines) adaptors. Data are modelled by a Weibull psychometric function, using the psignifit toolbox (ver. 2.5.6) for Matlab (http://bootstrap-software.org/psignifit/). DIFFERENT-target and adaptor are presented in opposite hemifields. SAME-target and adaptor are presented in the same location.

(Kovács et al., 2005) and suggests that facial aftereffects consist of a position-invariant and non-invariant component after long adaptation durations.

Short-term adaptation also evoked significant aftereffects (main effect of adaptation condition: $F(2, 1650) = 29$, $p < 0.009$). However, in contrast to the long-term adaptation conditions in the short-term adaptation conditions the size of the adaptation effect did not differ significantly between the SAME and DIFFERENT conditions ($p = 0.11$, post-hoc t-test). This suggests that the facial aftereffects evoked by short-term adaptation are entirely position invariant.

Adaptation duration had a significant effect on the strength of facial aftereffects: comparison of the long-term and short-term adaptation conditions revealed that the test faces were judged more masculine after long-term adaptation than after short-term adaptation condition (main effect of adaptation duration ($F(1, 1650) = 87$, $p < 0.00001$). The difference in the strength of the facial aftereffects between long-term and short-term adaptation was more pronounced in the SAME as compared to the DIFFERENT condition (interaction of adaptation condition and adaptation time: $F(1, 1650) = 4$, $p < 0.05$).

3.2. ERP results

3.2.1. ERP responses over the hemisphere contralateral to the test stimuli

Fig. 3 shows the pooled grand average ERPs obtained on the occipito-temporal electrodes. We found strong adaptation effects for both short- and long-term adaptation conditions (Fig. 4a).

The onset of the adaptation effects—as measured by a point-by-point t-test on the grand average ERPs obtained in Control and the long-term adaptation conditions—was very similar for each condition: 117, 119 and 109, 106 ms for the long-term adapted SAME and DIFFERENT conditions over the right and left hemispheres, respectively.

The amplitude of the N170 component was smaller both in the long-term and in the short-term adaptation conditions than in the control condition for both hemispheres (main effect of adaptation condition: $F(2, 120) > 14$; $p < 0.0001$).

In the case of short-term adaptation condition the onset of the adaptation effects measured on the N170 component was at 119, 117 and 111, 114 ms for the SAME and DIFFERENT conditions over the right and left hemispheres, respectively.

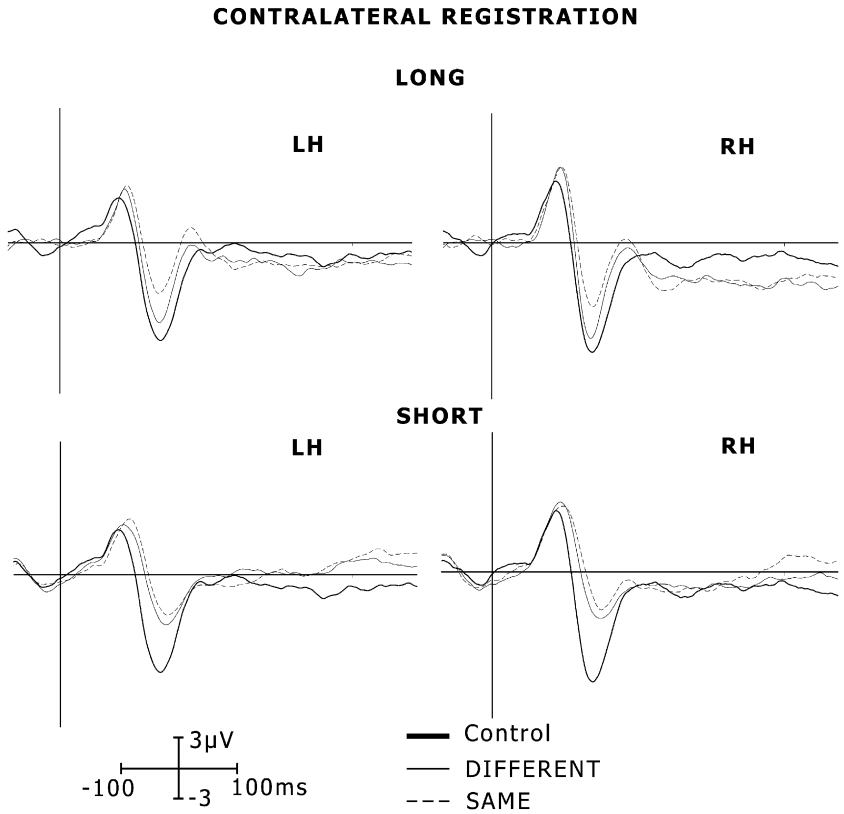

Fig. 3. Grand average ERPs recorded for contralateral target stimuli displayed between −100 and 500 ms at occipito-temporal sites for the Control (thick line), DIFFERENT (thin line) and SAME (dashed line) conditions. Upper panel: 5000 ms adaptation time, lower panel: 500 ms adaptation time. For demonstration purposes PO7, P7 and P9 was pooled together for the LH and PO8, P8 and P10 electrodes for the RH. LH, left hemispherium; RH, right hemispherium.

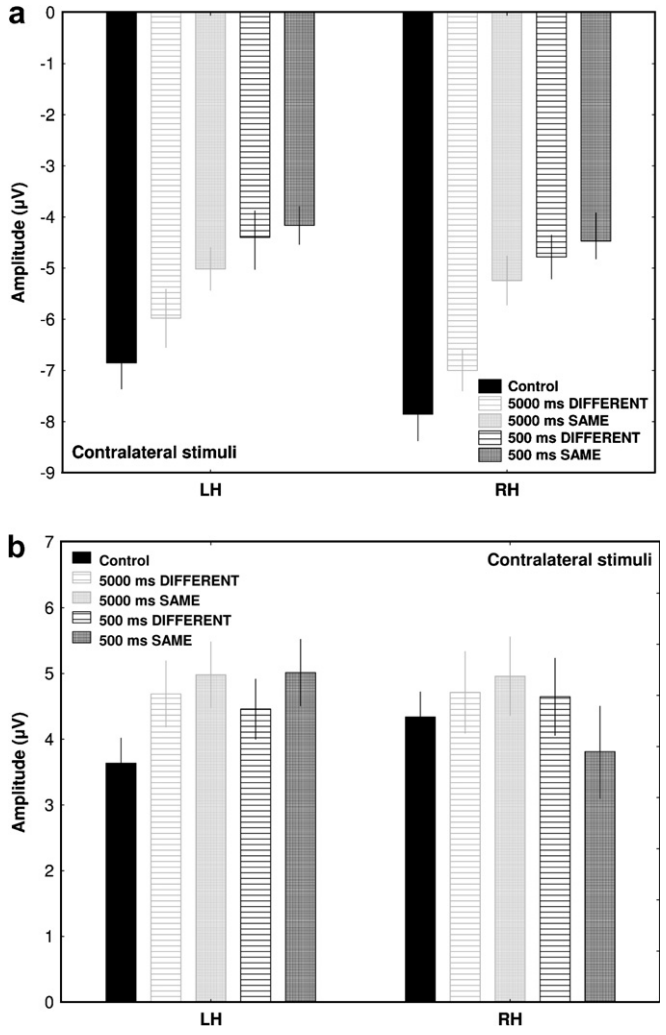

Fig. 4. The amplitudes of the N170 (a) and P100 (b) components for the three left (LH) and three right (RH) occipito-temporal channels in the contralaterally presented test stimuli in the long-term and short-term adaptation conditions (mean and standard errors).

When comparing the magnitude of N170 adaptation effects in the SAME and DIFFERENT conditions after long-term adaptation we found significantly lower amplitudes in the SAME than in the DIFFERENT conditions (post-hoc t-tests: $p < 0.00001$ and $p < 0.005$ for the right and left hemispheres, respectively). However, in the case of short-term adaptation conditions, there was no such difference in N170 amplitudes between the SAME and DIFFERENT adaptor-target arrangements, in neither hemispheres (post-hoc t-tests: $p < 0.08$ and $p < 0.1$ for the right and left hemispheres, respectively).

The observed behavioral adaptation effect correlated significantly only with the adaptation effect on the N170 amplitude after long-term adaptation ($r = 0.36$, $p < 0.05$).

The amplitude of the P100 component was larger after long-term adaptation over the left hemisphere (Fig. 4b, main effect of adaptation condition: $F(2, 38) = 9$; $p < 0.001$). Although short-term adaptation caused some increase of the amplitude of the left P100 components as well, but this effect was not significant ($F(2, 38) = 2.5$, $p = 0.09$).

More importantly, we have not observed significant differences in the adaptation effects on P100 amplitudes between the SAME and DIFFERENT conditions neither for the long-term nor for the short-term adaptation conditions over neither hemispheres (post-hoc t-tests: $p > 0.2$ for all comparisons).

These results suggest, that although long-term adaptation produces some moderate adaptation effects on the, P100 component of the ERP responses (in accordance with our previous results (Kovács et al., 2005)) this effect is similar for position-specific and position-invariant situations, thus cannot explain the observed differences in the N170 ERP component.

The fact, that the N170 and P100 adaptation effects reflect different adaptation mechanisms is supported further by the fact, that the P100 and N170 amplitudes showed no significant correlations neither on the left ($r = 0.04$, nor on the right side ($r = -0.06$).

Regarding the N170 latencies (Table 1) in the long adapted condition the main effect of adaptation condition was significant over the right hemisphere ($F(2, 120) = 9$, $p < 0.0002$) while no differences were found for the left hemisphere ($F(2, 120) = 0.6$, $p = 0.55$).

After short-term adaptation the latencies were also significantly larger than in the Control condition (main effect of adaptation condition: $F(2, 120) = 36$, $p < 0.0001$ and $F(2, 120) = 23$, $p < 0.0001$ for right and left hemispheres, respectively).

The latency of the P100 component (Table 2) was significantly longer after both short- and long-term adaptation

Table 1
The latency values (mean and standard error) of N170 ERP component for the left and right hemispheres in the different conditions

N170	Contralateral		Ipsilateral	
	LH	RH	LH	RH
Control	168 (2.3)	170 (1.9)	173 (1.7)	177 (1.6)
Long DIFFERENT	165 (1.9)	168 (1.3)	164 (1.7)*	170 (1.2)*
Long SAME	167 (2.1)	175 (2.2)*	165 (1.7)*	176 (1.6)
Short DIFFERENT	176 (2.4)*	186 (2.2)*	176 (2.4)	188 (2.3)*
Short SAME	179 (2.2)*	183 (2.4)*	177 (2.0)	184 (2.5)*

Asterisks sign significant differences from the appropriate control condition by Fishers post-hoc tests ($p < 0.01$).

Table 2
The latency values (mean and standard error) of P100 ERP component for the left and right hemispheres in the different conditions

P100	Contralateral		Ipsilateral	
	O1	O2	O1	O2
Control	114 (3.8)	113 (1.9)	115 (3.2)	119 (4.0)
Long DIFFERENT	118 (3.2)*	119 (2.4)*	117 (2.3)	120 (3.9)
Long SAME	121 (3.8)*	121 (2.1)*	118 (2.4)	120 (3.5)
Short DIFFERENT	123 (3.7)*	120 (2.4)*	126 (4.2)*	127 (3.5)*
Short SAME	124 (3.7)*	120 (3.7)*	123 (3.9)*	126 (3.0)*

Asterisks sign significant differences from the appropriate control condition by Fishers post-hoc tests ($p < 0.01$).

(main effects of adaptation condition $F(2, 38) > 4.2$, $p < 0.01$ for all four comparisons).

As for SAME and DIFFERENT conditions the N170 latencies were longer in the SAME condition than in the DIFFERENT conditions (post-hoc *t*-tests: $p < 0.00004$ for left and right hemispheres) after long-term adaptation, while no such differences were observed after short-term adaptation (post-hoc *t*-tests: $p = 0.6$ and $p = 0.1$ for right and left hemispheres, respectively).

3.2.2. ERP responses over the hemisphere ipsilateral to the test stimuli

Fig. 5 presents the pooled grand averages during ipsilateral stimulus presentations.

The point-by-point *t*-tests revealed that the onset of this effect was 134, 168 and 125, 116 ms for the long-term adapted SAME and DIFFERENT conditions over the right and left hemispheres, respectively. In case of the short-term adaptation the onsets were 112, 116 and 125, 120 ms for the short-term adapted SAME and DIFFERENT conditions over the right and left hemispheres, respectively.

The N170 amplitudes (Fig. 6a) were lower in the adapted conditions than in the control condition for both hemispheres and for both adaptation durations (main effect of adaptation condition for all four comparisons: $F(2, 120) > 9$; $p < 0.0001$).

No differences were found between the SAME and DIFFERENT adaptor-target arrangements, although in case of short-term adaptation there was a tendency for larger N170 amplitudes in case of DIFFERENT than in case of SAME condition (long-term adaptation: post-hoc *t*-tests, $p < 0.7$ and $p < 0.3$ for the right and left hemispheres, respectively; short-term adaptation $p < 0.1$ and $p < 0.07$).

Long-term adaptation caused a significant increase on the P100 component in case of the ipsilateral stimuli (Fig. 6b; main effects of adaptation: $F(2, 38) = 7.9$; $p < 0.001$ and $F(2, 38) = 6.8$; $p < 0.003$ for the left and right sides, respectively). SAME amplitudes were larger than DIFFERENT ones over the left hemisphere (post-hoc *t*-test: $p < 0.04$).

After short-term adaptation the P100 amplitude difference, was only significant over the right hemisphere ($F(2, 38) = 1.3$; $p = 0.28$ and $F(2, 38) = 4.8$; $p < 0.01$ for left and right, respectively) and no difference was observed between SAME and DIFFERENT (post-hoc *t*-tests: $p = 0.1$ and $p = 0.8$ for right and left hemispheres, respectively).

P100 and N170 amplitude values showed no significant correlations over the ipsilateral sites either ($r = 0.07$ and $r = 0.08$ for the left and right hemispheres, respectively).

The N170 latencies (Table 1) in the long-term adaptation condition showed a significant main effect of adaptation condition because of the shorter latencies after

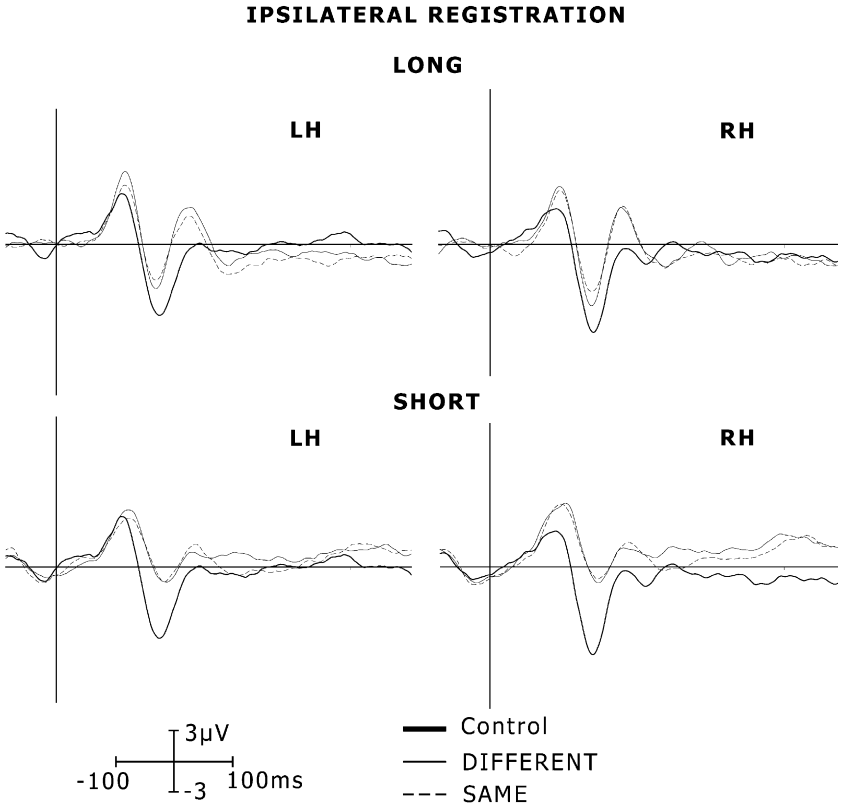

Fig. 5. Grand average ERPs recorded for ipsilateral test stimuli displayed between −100 and 500 ms at occipito-temporal sites for the Control (thick line), DIFFERENT (thin line) and SAME (dashed line) conditions. Upper panel: 5000 ms adaptation time, lower panel: 500 ms adaptation time.

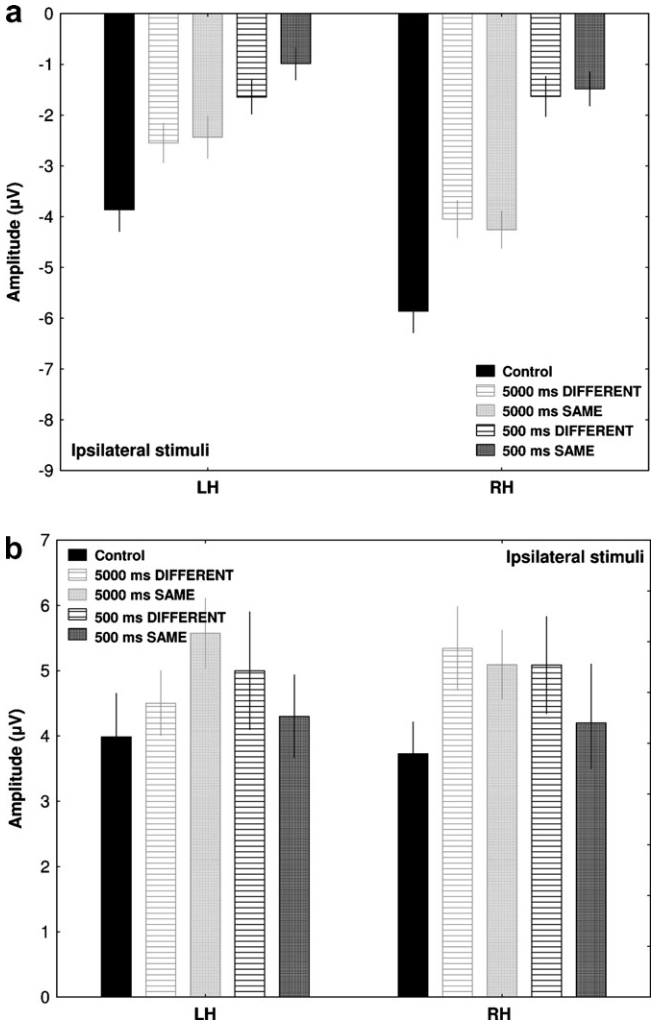

Fig. 6. The amplitudes of the N170 (a) and P100 (b) components for the three left (LH) and three right (RH) occipito-temporal channels in the contralaterally presented target stimuli in the long-term and short-term adaptation conditions (mean and standard errors).

adaptation compared to Control over both hemispheres ($F(2, 120) = 9$, $p < 0.00001$) and ($F(2, 120) = 11$, $p < 0.0006$) for left and right). SAME and DIFFERENT N170 latencies showed no differences (post-hoc t-tests: $p = 0.2$ and $p = 0.7$ for right and left hemispheres, respectively).

In case of short-term adaptation the latencies were longer than for control, but only over the right hemisphere (main effect of adaptation condition: $F(2, 120) = 15$, $p < 0.00001$ for right and $F(2, 120) = 2$, $p < 0.2$ for the left). Just like with long-term adaptation SAME and DIFFERENT latencies were similar (post-hoc t-tests: $p = 0.4$ and $p = 0.3$ for right and left hemispheres, respectively). SAME and DIFFERENT N170 latencies showed no differences (post-hoc t-tests: $p = 0.7$ and $p = 0.5$ for right and left hemispheres, respectively).

The P100 latencies (Table 2) showed no significant main effect of adaptation condition after long-term adaptation ($F(2, 38) = 1.6$, $p = 0.2$ and $F(2, 38) = 0.2$, $p = 0.9$ for left and right, respectively). Short-term adaptation, however, increased the P100 latencies ($F(2, 38) = 7.5$, $p < 0.003$ and $F(2, 38) = 8.6$, $p < 0.002$ for left and right, respectively). SAME and DIFFERENT were similar for both short- and long-term adaptation, over both the left and right hemispheres (post-hoc t-tests: $p > 0.3$ for all four comparisons).

4. Discussion

The results of the present study show that—in agreement with previous results (Kovács et al., 2005)—long-term (5 s) face adaptation evokes aftereffects consisting a position-invariant as well as a position-specific component. As a result of adaptation to a female face, test faces were judged more masculine when they were displayed in the same location as the female adaptor face, as compared to that when they were presented in the opposite visual hemifield. However, in conditions when the adaptation time was reduced to 500 ms the resulting face aftereffects were found to be entirely position-invariant and no position-specific adaptation effects were observed. In accordance with our behavioral results, the N170 ERP component—recorded over the hemisphere contralateral to the test stimulus—shows position-specific component only in the case of long-term adaptation: adaptation effects expressed in the N170 amplitude are larger for SAME than for DIFFERENT adaptor-test stimulus arrangement only in the long-term, but not in the short-term adaptation conditions.

The fact, that the N170 adaptation effects, recorded for ipsilaterally presented stimuli were always similar for SAME and DIFFERENT replicates our previous data (Kovács et al., 2005) and suggest, that the behavioral facial adaptation effects might be mediated primarily by the adaptation of the shape-selective neural processes in the hemisphere contralateral to the test face stimulus.

Recent fMRI studies suggest that adaptation processes may operate on different timescales in different cortical areas. It was found that obtaining orientation-tuned adaptation signal measurable with fMRI in visual cortical area V1 requires long-term (several seconds) adaptation (Fang et al., 2005), whereas, in the extrastriate cortical areas, adaptation effects were observed both after long-term as well as short-term adaptation (Henson, 2003a). These results suggest that duration of adaptation is a critical factor, which can determine whether adaptation effects will be observed in a given cortical area. Moreover, Fang et al. (2006) has shown that adaptation duration can also affect the properties of fMRI adaptation effects. Only long-term (5000 ms) adaptation effects were found to be selective to the viewpoint of the face, whereas short-term (300 ms) adaptation effects were viewpoint independent The results of the present study are in line with these previous findings, by showing that only the position-invariant face-selective processes are adapted after both short-term and long-term adaptation, whereas adaptation of the neurons responsible

for position-specific coding of facial information requires long-term adaptation.

Although, our results do not allow us to determine the exact neural site of the position-specific and position-invariant component of face aftereffects, it is important to point out that both components are reflected in the later, N170 component of the face-evoked ERP responses. Since, the results of several previous studies point to the conclusion that N170 reflects the structural coding of face stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004; Rossion et al., 1999, 2000) and not the low level processing of their basic visual attributes (contrast, orientation, etc.), our findings suggest that even the position-specific component of the facial aftereffects originate from adaptation processes at the higher, shape-specific stages of visual processing. Indeed, Melcher (2005) measured visual form aftereffects across separate fixations and found large transfer of face adaptation, along with spatially non-specific effects, suggesting spatiotopic, rather than retinotopic coding. Furthermore, recent single-unit recording studies have provided evidence that some positional information is preserved in the inferior temporal cortex of the macaque brain (for review see Rousselet, Thorpe, & Fabre-Thorpe, 2004). It was found that the receptive fields of inferior temporal neurons can differ in size, have ''hot spots'', where they are most sensitive to stimulation, and are typically biased towards the contralateral hemifield (DiCarlo & Maunsell, 2003; OpDeBeeck & Vogels, 2000; Rolls, Aggelopoulos, & Zheng, 2003). Adaptation of high-level cortical neurons of the human brain, having similar properties could explain that facial aftereffects are only partially position invariant. However, further fMRI investigations are required to localize directly these position-specific and position invariant adaptation effects and to uncover whether they reflect adaptation of different face-selective neural populations of the same or different visual cortical areas.

We found some adaptation effects (enlarged amplitude and elongated latencies) on the earlier, P100 component of the ERP as well using 5000 ms adaptation time. This is in line with our previous findings (Kovács et al., 2006) and with the current literature (Itier & Taylor, 2004), that suggest that this component might reflect the holistic processing of a face as a face. However, this effect was similar for SAME and DIFFERENT, suggesting that it reflects different mechanisms than the N170 component. After short-term adaptation no effect was observed on the amplitude of P100 while its latency was significantly longer than in the control condition. Such adaptation-related response latency increases have been shown previously for motion adaptation (Hoffmann, Unsold, & Bach, 2001). This suggests that the P100, in addition to the early visual analyses (Gomez, Clarck, Luck, Fan, & Hillyard, 1994; Heinze et al., 1994), to some extent also reflects shape-selective neural processing and indicates that its latency might be sensitive to the state of adaptation at these higher processing stages.

Our results have important implications regarding the recently described face competition effect (Jacques & Rossion, 2004, 2006; Rossion, Kung, & Tarr, 2004). Jacques and Rossion (2004, 2006) found that neural responses (decreased N170 amplitude) to a face stimulus are reduced when it is displayed in the presence of another face stimulus, which has been on the screen for about 500–700 ms before the presentation of the test face. The main difference between the paradigm used by Jacques and Rossion (2004, 2006) and our short-term adaptation condition is that in our experiments the first face stimulus is removed 500 ms prior to the presentation of the second (test) face stimulus, whereas in their experiments it stays on the screen during the presentation of the second (target) face. Since, in the present study we found strong position-invariant short-term adaptation effects on the amplitude of the N170 evoked by the test stimulus, it appears reasonable to suppose that such adaptation effects might also have contributed to the observed N170 amplitude reduction in the experiments by Jacques and Rossion (2004, 2006).

In conclusion, our results suggest that long-term exposure to a face stimulus results in adaptation of a position-specific population of face selective neurons in addition to the position invariant neural population, which is adapted both in the case of short- and long-term adaptation. These findings imply that adaptation duration is a critical factor, which should be taken into account during the interpretation of behavioral as well as neural effects of visual adaptation. Moreover, manipulating adaptation duration provides an opportunity to selectively adapt neural processes at different stages of visual processing and investigate their stimulus selectivity.

Acknowledgments

This work was supported by grants from the Hungarian Scientific Research Fund to G.K. (T049467) and to Z.V. (T048949) by the European Commission NEST project 028714 and by the Bolyai Fellowship to Z.V. We thank Judith Máthé and Zsanett Zsadányi-Nagy for help in running the experiments. We thank the two anonymous reviewers for their comments on the previous version of the manuscript.

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